Report on the Anatomy of the Tsetse-fly (Glossina palpalis).

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The following description is based upon dissections and preparations made in the laboratory of the Sleeping Sickness Commission at Entebbe since my arrival here at the beginning of April. I hope on my return to England to work up my material into a detailed memoir on the anatomy and histology. Time does not suffice for me to complete my work out here, but it seemed worth while, nevertheless, to bring forward as soon as possible a brief description of the general anatomy of the fly, and especially of its digestive tract, on account of its importance for the study of the evolution of the trypanosomes of Sleeping Sickness, and other tsetse-fly diseases, within the body of their invertebrate host.

In this paper I do not propose to attempt to deal with either the muscular system or the respiratory tracheal system. The former of these is so complex that much more time would be required for working it out than I could afford to spend, and it is, moreover, of little or no importance for the aim in view; while the tracheal system, or at least its finer branches, are so intimately connected with the fat-body, which here, as in other insects, fills up the body-cavity, that in the process of clearing up and laying bare the organs, the tracheæ are for the most part removed. Special muscles or tracheæ will be mentioned in places, but otherwise no account will be taken of these two systems.

The drawings illustrating this memoir are to be regarded as semi-diagrammatic, but all details in them have been traced from sketches made with the camera lucida from actual dissections, and therefore claim to be true to nature and accurate as regards scale and proportions. For help in the preparation of these drawings I am much indebted to my colleague, Mr. F. Tulloch, R.A.M.C., who also kindly cut some sections for me. Mr. Tulloch has also made some dissections of *Stomoxys*, comparison with which has thrown light on some points in *Glossina*; Mr. E. Degen, who came out with me, has also helped me in various ways.

Since I have no access out here to any literature or works of reference dealing with insect-anatomy, I am unable to make this account comparative,

or to state how far *Glossina* differs from other Diptera as regards internal structure. I shall content myself, therefore, with describing the facts observed by me in a purely objective manner.

In the following description I shall employ the term *waist* for the narrow peduncle connecting the thorax and abdomen, and *neck* for the still narrower connection between head and thorax.

1. *The Nervous System of Glossina*, as of other Diptera, is concentrated into two masses, one situated in the head, the other in the thorax.

The brain (fig. 1) consists of the two large cerebral ganglia (*S. O. G.*) giving off laterally the still larger optic lobes (*Op. l.*), from which arise the optic nerves. The dissection of the brain and its nerves is rendered somewhat difficult by the large air-sacs, dilatations of the tracheal system, contained in the head. From the anterior side of the cerebral ganglia various nerves are given off: first, a median nerve of moderate size to the three ocelli (*oc. n.*), arising from the furrow between the two cerebral ganglia, and apparently swelling out into a small ganglion; secondly, a pair of nerves to the antennæ, arising about half-way down the front of the brain on each side; thirdly, a pair of small nerves which innervate the muscles of the pharynx, arising near the base of the brain; and lastly, a pair of nerves to the proboscis, which arise from the base of the brain, run forward ventrally to the pharynx, giving off nerves at this point to the muscles of the proboscis, and finally enter the bulb of the proboscis, to be distributed to the mouth-parts (fig. 5, *n. p.*).

From the posterior surface of the brain, near its base, the two stout connectives (fig. 1, *Cn.*) arise, and pass down on each side of the greatly narrowed œsophagus, after which they unite almost immediately to form a single broad band of nerve-tissue, which runs back through the neck to join the thoracic ganglion-complex. From this connective band, as it may be termed, there arises, immediately after it enters the thorax, a slender pair of nerves, which form a delicate plexus with the first pair of prothoracic nerves arising a short way behind them (fig. 1, *Cn. n.*).

The connective band often appears distinctly double at its junction posteriorly with the thoracic ganglion-mass, which lies immediately ventral to the stomach, the anterior end of the former being a short distance behind that of the latter. It is a mass of considerable thickness in the dorsoventral direction, and appears more or less pear-shaped in a dorsal view, but seen from the ventral side its anterior end appears truncated. When stained, cleared, and mounted in Canada balsam, it is seen distinctly to be composed of three pairs of large ganglia united together, corresponding to the three segments of the thorax, behind which a small mass of ganglion-cells,

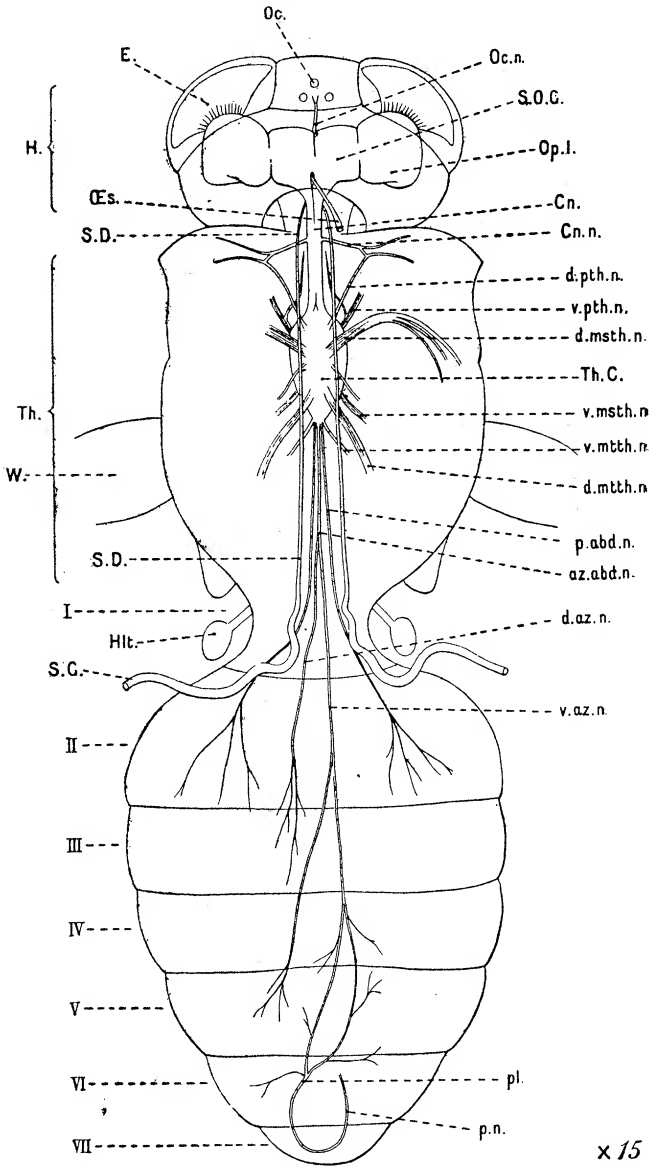

FIG. 1.—General Sketch of the Nervous System, dorsal view. The top of the head is pushed forward and downward as far as possible, to show the brain. A portion of the œsophagus and the salivary ducts are also represented, the salivary gland being supposed to be turned outwards from the abdomen and cut off near the origin of the ducts.

All lettering relating to the nervous system has been placed on the right of the figure, that referring to other parts on the left. *H.*, head ; *Th.*, thorax ; I—VII, the segments of the abdomen ; *Oc.*, ocelli ; *E.*, eyes ; *Œs.*, œsophagus (cut off) ; *S. D.*, *S. D.*, salivary duct ; *W.*, origin of wings ; *Hlt.*, halter ; *S. G.*, salivary gland ; *Oc. n.*, ocellar nerve : *S. O. G.*, right cerebral ganglion ; *Op. l.*, right optic lobe ; *Cn.*, connectives ; *Cn. n.*, nerve from the connective forming a plexus with : *d. pth. n.*, dorsal prothoracic nerve ; *v. pth. n.*, ventral prothoracic nerve ; *d. msth. n.*, *v. msth. n.*, dorsal and ventral mesothoracic nerves ; *Th. c.*, thoracic ganglion complex ; *d. mtth. n.*, *v. mtth. n.*, dorsal and ventral metathoracic nerves ; *p. abd. n.*, paired abdominal nerve ; *az. abd. n.*, azygos abdominal nerve ; *d. az. n.*, dorsal branch of the azygos nerve ; *v. az. n.*, ventral branch of the azygos nerve (genital nerve) ; *pl.*, plexus formed by the genital nerve ; *p. n.*, nerve to penis.

representing the abdominal nervous system, forms the posterior-pointed termination of the thoracic complex.

From each of the thoracic ganglionic centres arise two nerves, one dorsal and one ventral, so that altogether six pairs arise from the body of the thoracic complex, which are distributed to their proper regions of the thorax. From the posterior end of the thoracic complex arise three nerves, one median unpaired, and two lateral paired, which pass backwards into the abdomen.

The greater part of the thorax of the fly is a mass of muscle, and as the muscles have to be removed in order to display the other organs in the thorax, the terminations and finer branches of the nerves are torn away from them. Hence it is impossible to describe accurately the destinations of these nerves without a detailed study of the musculature, which, as already stated, I have not made. It would appear, however, that the three ventral pairs of thoracic nerves innervate the legs and their muscles.

The dorsal prothoracic nerves (fig. 1, *d. pth. n.*) are very slender, and, as already stated, form an anastomosis with the nerves from the connectives. The ventral prothoracic nerves (*v. pth. n.*) are of moderate size.

The dorsal mesothoracic nerves (*d. msth. n.*) are very large, being in fact the stoutest nerves in the body. They run slantingly forward, then curve round till they run in a backward direction, and appear to be distributed to the wing-muscles. A small nerve arises from the ganglion close behind the origin of the dorsal mesothoracic nerves, and runs backwards in a dorsal direction. It is drawn in fig. 1, but not lettered, and is probably to be regarded as a branch of the dorsal mesothoracic nerve. The ventral mesothoracic nerves (*v. msth. n.*) are also of fairly large size.

The dorsal metathoracic nerves (*d. mtth. n.*) are large, the ventral ones (*v. mtth. n.*) of moderate size.

The three abdominal nerves run at first straight backwards, and almost parallel to each other, to the waist. Before reaching it the median nerve (*az. abd. n.*) has divided into a smaller dorsal and a larger ventral branch. After passing through the waist the two lateral nerves (*p. abd. n.*) diverge outwards to the sides of the abdomen and break up into numerous branches.

The dorsal branch of the median nerve is distributed to organs situated dorsally in the abdomen. The ventral branch of the median nerve is the nerve of the generative organs. In the male I have found that its branches unite to form a plexus (fig. 1, *pl.*), apparently containing a small ganglion, which gives off nerves in various directions, and from which a fairly stout nerve (*p. n.*) arises and follows the ductus ejaculatorious in its tortuous

course, till it finally enters with it the penis, the muscles of which it innervates. In the female a similar plexus appears to be formed, but owing to the dense tangle formed by the fat-body, uterine glands, and Malpighian tubules, I have not succeeded in dissecting out its finer details.

2. *The Digestive Tract.*—Since the proboscis, buccal cavity, and pharynx have been thoroughly described in Austen's monograph by Hansen, whose account I can but confirm, I commence my description with the œsophagus. This portion of the alimentary canal (figs. 1 and 2, *Œs.*) runs first of all in an upward direction from the pharynx (*Ph.*), then bends sharply round and passes backwards through the brain. The first portion of the œsophagus is dilated, but slightly compressed, appearing of greater calibre in a dorsal than in a lateral view. After bending round, it narrows rapidly, and the portion which passes through the brain is of extreme tenuity, scarcely, if at all, of greater calibre than the salivary ducts. Behind the brain the œsophagus widens, at first very gradually, then, after entering the thorax, more rapidly, till it joins the stomach, into which it opens ventrally, breaking through the floor slightly in front of the point at which the thoracic intestine arises dorsally. From the point at which the œsophagus opens into the stomach, the duct of the sucking stomach arises.

The stomach, which marks the commencement of the mesenteron, has a peculiar and very characteristic form (fig. 2, *St.*). Seen from the dorsal aspect, it appears roughly oblong in form, with a bevelled anterior edge, and the upper surface more or less saddle-shaped, *i.e.*, convex in the transverse section, concave in the longitudinal direction. Seen from below, its lateral edges appear wrapped round the œsophagus and the duct of the sucking stomach, on which it rides, as it were. From the dorsal side of the stomach, about the middle of its length, arises the intestine, the first part of which (*Th. I.*) runs backwards through the thorax as a straight tube of even calibre, until it passes the waist. As soon as it enters the abdomen the intestine swells and becomes the strictly digestive portion of the alimentary canal.

The abdominal intestine is of great length, but until it reaches the proctodæum it cannot be divided into regions. It forms a number of complicated coils in the abdomen, and for purposes of description a number of limbs may be distinguished, each limb separated from the one next following by a more or less sharp bend (figs. 2 and 3).

The first limb (1) runs backwards along the abdomen in a dorsal situation, curving first slightly to the right, then more strongly to the left, until it reaches the fifth segment, where a sharp bend takes place forwards in a ventral direction. The second limb (2) curves round from left to right,

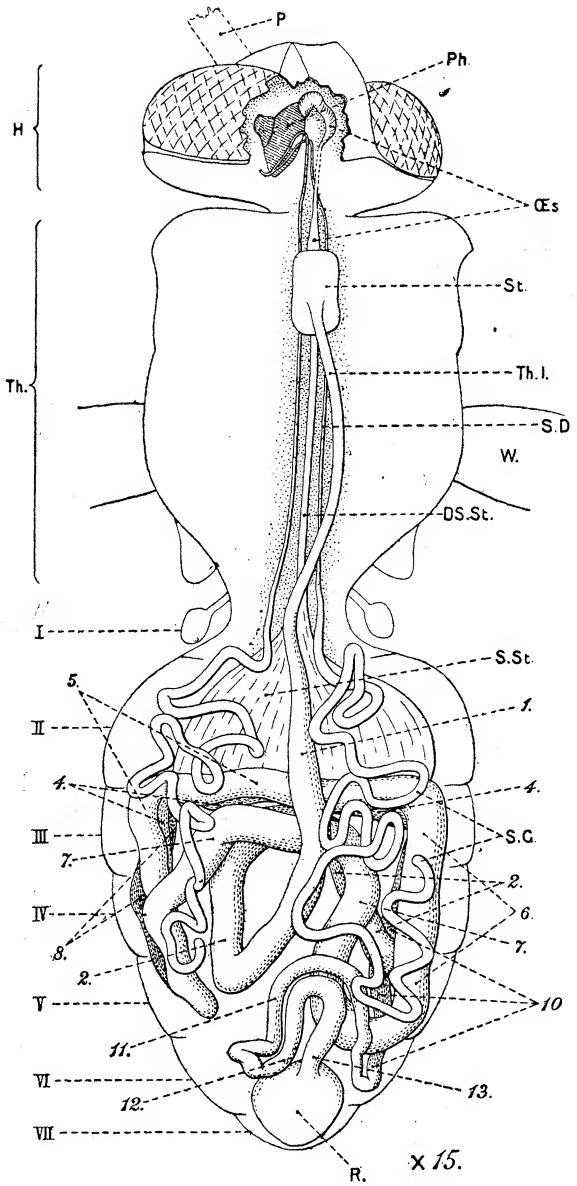

FIG. 2.—General View of the Digestive Tract, as seen in dorsal view without disturbing its parts. The heart and overlying tracheæ and fat-body are removed in the abdomen, also the muscles in the thorax, and the brain and other parts of the nervous system are omitted from the drawing. The head is turned round to the left, in order to show the pharynx, etc., in three-quarter side view.

Ph., pharynx; *Œs.*, œsophagus (the portion which passes through the brain being represented with a dotted outline); *St.*, stomach; *Th. I.*, thoracic intestine, pulled over to the right, in order to show the duct of the sucking stomach lying beneath it; *S. D.*, salivary duct; *DS. St.*, duct of: *S. St.*, the sucking stomach; *S. G.*, salivary gland (that on the right is drawn from a specimen in which the gland was more developed than in the case of that drawn on the left); 1—13, limbs of the abdominal intestine (see fig. 3); *R.*, rectum. Other letters as in the preceding figure.

running first anteriorly, then transversely, and lastly in a posterior direction. It is more ventral in situation, being placed below some of the succeeding coils. The third limb (3) is short, and runs straight forward on the right side from the fifth to the third segment. Not visible in fig. 2, its position is indicated in fig. 3. The fourth limb (4) turns at right angles, and runs

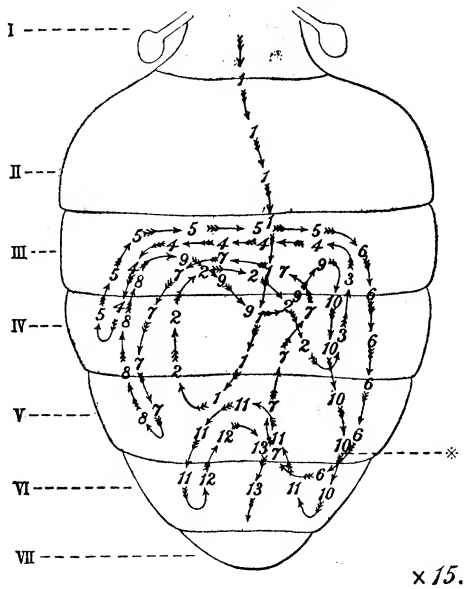

FIG. 3.—Diagram to show the various limbs (1—13) of the abdominal intestine, and their arrangement in the abdomen. The asterisk * denotes the point at which the Malpighian tubules arise in the tenth limb.

transversely across the body in the third segment, passing back a short distance into the fourth. The fifth limb (5) turns sharply back on the fourth and runs dorsally to it across the body again in the third segment. The sixth limb (6) turns back at a right angle and runs back on the right side of the body from the third to the sixth segment. The seventh limb (7) turns sharply forwards, then curves round in a roughly semi-circular course in the third segment, and finally runs backwards on the left side as far as the fifth segment. The fifth, sixth, and seventh limbs form together a well-marked loop, lying superficially, which is generally the most dilated portion of the intestine. The eighth limb (8) bends sharply forwards and downwards, and runs deep on the left side from the fifth to the third segment. The ninth limb (9) bends at right angles and runs at first transversely in the third segment, then curves back into the fourth, then forwards again into the third segment. The tenth limb (10) runs backwards along the right side of the body from the third to the sixth segment, and in the fifth segment gives off

the Malpighian tubules (*, fig. 3), so that from this point the gut must be regarded as proctodæum. The eleventh limb (11) runs from right to left in a semicircular curve occupying the fifth and sixth segments. From the origin of the Malpighian tubules to the end of the eleventh limb the gut is of small calibre, and may be called the ileum. The succeeding portion is thicker, and may be called the colon. It lies in the fifth and sixth segments, and forms the twelfth and thirteenth limbs (12, 13), both short and sharply bent one on the other. The ileum and colon lie dorsally in the body, and the colon passes into the capacious rectum (*R.*), which has four rectal glands (fig. 5, *r. gl.*) each supplied by a bunch of small tracheæ.

The appendages of the digestive tract are the salivary glands, the sucking stomach, and the Malpighian tubules.

The salivary glands (fig. 2, *S. G.*) commence, starting from their distal ends, as two long tubes, much coiled, and occupying a very superficial dorsal position in the abdomen on each side of the heart, above the alary muscles. Very transparent in the fresh condition, the salivary glands become glistening white in colour when put in alcohol. Only tracheæ and fat-body come between them and the dorsal body-wall. The coils of the tubes extend back as far as the fourth or fifth abdominal segment, but the distal extremity of the gland may lie further forward than this. With many twists and turns the tubes run forward to the waist and then pass into the thorax, at the same time diminishing rapidly in calibre, straightening out their coils, and descending to the ventral side of the body. From this point the salivary gland becomes the salivary duct (figs. 1 and 2, *S. D.*). The two ducts run a parallel course through the thorax, on a level with the duct of the sucking stomach, and on each side of it, passing under the stomach and above the thoracic ganglion (figs. 1 and 2). When they reach the neck, the salivary ducts become so extremely attenuated that their course through the head is very difficult to follow. As they enter the neck the ducts curve over towards each other, and pass under the connective nerve-band, thus parting company from the œsophagus, which passes above the connective. The ducts pass under the brain and then under the pharynx.

If the head of a fly be examined from below, there will be found, immediately behind the bulb of the proboscis, an area covered by soft flexible integument, which recalls the soft skin at the base of a parrot's beak, and has a similar function, that is to say, to allow free play for the movements of the proboscis. When the proboscis is bent down, in the attitude it assumes when the fly is drawing blood, the soft skin forms a fold over the bulb, and when the proboscis points forward, in the attitude of repose, enclosed in the sheath formed by the two palpi, then the soft

integument is stretched. If this flexible skin be removed, a cavity is exposed lying below the pharynx (fig. 4, *Ph.*), across which run the nerves

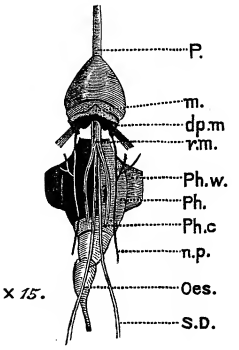

FIG. 4.—Dissection of Pharynx, Proboscis, Salivary Ducts, etc., ventral view.

P., proboscis ; *m.*, soft integument cut away behind the bulb of the proboscis ; *dp m.*, depressor muscle of the proboscis ; *r. m.*, retractor muscles ; *Ph.*, pharynx ; *Ph. w.*, chitinous wings of the pharynx ; *Ph. c.*, membranous continuation of the ventral wall of the pharynx, to which the retractor muscles are attached ; *n. p.*, nerve to the proboscis ; *Œs.*, œsophagus ; *S. D.*, salivary duct.

to the proboscis (*n. p.*), a pair of retractor muscles uniting anteriorly (*r. m.*) and the two delicate salivary ducts (*S. D.*). The last-named remain perfectly distinct and separated from one another until they pass dorsally to the median muscle formed by the two united refractors. A stained preparation, which I have cleared and mounted in Canada balsam, shows the two ducts uniting into a single duct above this muscle. In *Stomoxys*, according to Hansen's description, the two salivary ducts unite into a median duct much further back than I have found to be the case in *Glossina*. Hansen, it may be noted in passing, speaks always of the thoracic salivary gland,* but in *Glossina* these glands are not thoracic, and in *Stomoxys* they are partly abdominal. The immensely powerful muscles of flight, filling up the thorax, are probably the cause of the glands being shifted back into the abdomen. To follow the further course of the salivary duct after it enters the proboscis, sections would be required, which I have not made, since Hansen has already described the duct as opening on the hypopharynx, as in all other insects.

The sucking stomach is morphologically a ventral diverticulum of the distal end of the œsophagus, which is placed in the two anterior segments of the abdomen, its connection with the œsophagus being drawn out into a long

* Austen also states ("Monograph," p. 35) that "the salivary gland [of Diptera] . . . is always situated in the *thorax*." (The italics are Austen's.)

slender duct traversing the thorax. The sucking stomach in the ordinary condition of the fly is filled with gas, but shortly after feeding it is found filled with blood.

The duct of the sucking stomach arises, as already stated above, from the œsophagus, at the point at which the latter communicates with the stomach, in such a way as to appear as a direct continuation of the œsophagus, the opening into the stomach having rather the appearance of a dorsally-directed diverticulum. At the point where the communication with the stomach occurs, the sides of the stomach are folded down ventrally so as to wrap completely round the duct, meeting below it, and forming a complicated system of cavities into which the fat-body intrudes.

When the duct passes the waist, it expands rapidly to become the capacious sucking stomach (figs. 2 and 5, *S. St.*), which has delicate walls, provided with a layer of unstriped muscles disposed irregularly.

The Malpighian tubules (*M. t.*, *M. t.*, fig. 5) arise by a pair of main stems given off from opposite sides of the 10th limb of the abdominal intestine. Each of these stems very soon divides into two again. In *Glossina* these tubules are excessively long, and so entangled with the fat-body and other organs that it is impossible to unravel them for their whole length, but since they are never observed to branch again, after their origin from the two main stems, it may be inferred that, as in other Diptera, there are in all four Malpighian tubules, disposed in this case in two couples, each couple coming off from a common stem. When the dorsal integument of the abdomen is removed, it can generally be observed without difficulty that two of the Malpighian tubules have thickened terminations, which lie close alongside the heart in the pericardial sinus right and left. In some specimens of *Glossina* these two tubules are not conspicuously thickened, but their position is constant. In no case do they exceed the salivary glands in thickness. It is evident that these two tubules must be of physiological importance for purifying the blood in the pericardial sinus. Mr. Tulloch has found in *Stomoxys* the same two pericardial Malpighian tubules, thickened to such an extent as to greatly exceed in calibre the salivary glands. Mr. Tulloch also found, and I was able to confirm his observation, that the two pericardial tubules of *Stomoxys* were a couple, arising both from one of the two stems on one side of the gut. The Malpighian tubules being much shorter in *Stomoxys* than in *Glossina*, it was possible to dissect out the two pericardial tubules of the former as far as their common origin from the gut, at which point they were detached, stained, and mounted in Canada balsam, thus putting this somewhat unexpected result beyond all doubt. Whether the two pericardial Malpighian tubules of *Glossina* are also, like those of *Stomoxys*, a couple with

a common origin, cannot be stated with complete certainty, but it seems at least highly probable. The morphological significance of this fact is, perhaps, that the two common stems of the Malpighian tubules are not to be considered as arising right and left from the gut, but as dorsal and ventral in origin. I have not succeeded in finding the distal extremities of the two remaining tubules, but they appear to pass down towards the ventral side of the abdomen and to be entangled with the genital organs, the dissection of which they help to render difficult.

3. *The Genital Organs* lie in both sexes close to the ventral side of the body in the hinder segments of the abdomen.

The male organs (fig. 5) consist of two pairs of tubes, greatly convoluted for a whole or a part of their course, which open all together into an unpaired tube, the ductus ejaculatorius, which in its turn passes to the external organs of generation and opens on the penis.

Commencing with the paired portions of the male apparatus, it is observed that the two tubes on either side differ markedly from one another. One pair, placed most posteriorly, is tightly wound and has the coiled portion pigmented. The other pair, more anterior, forms a looser coil and is without any pigment. I identify the former as the testis, the latter as the vesiculæ seminales.

Each testis commences with a delicate white filament (*t. f.*), embedded in the fat-body and difficult to trace. I have not succeeded in finding where the free end of the filament is attached; in dissections it appears to be loose. The filament passes on into the tightly coiled pigmented tube, which forms a conspicuous, compact, brown body, the testis (*T.*). In one dissection I succeeded accidentally in uncoiling the testis by pulling inadvertently on the filament when trying to remove the fat-body. It was then seen that each testis is a whitish coiled tube enveloped in a pigmented brown coat, which crumbles easily into a brown powder. In specimens that have been long in alcohol also the pigmented coat often sticks to the surrounding fat-body and comes away from the testis. The proximal part of the testicular tube is dilated and forms the testis proper; the distal portion is of smaller calibre and more tightly coiled, forming an epididymis, from which the tube is continued as the vas deferens (*V. d.*). The latter is a white, straight, or but slightly sinuous tube. The brown pigment of the testis is continued a very short way down the vas deferens, and ends abruptly.

Each vesicula seminalis (*V. s.*) is a white tube, commencing with a blind end. A short distance from the commencement the tube is slightly thickened for a short distance. There is nothing to bind the coils together, nor any pigment, as in the testis. Distally the tube straightens out to open into the unpaired duct of the generative system.

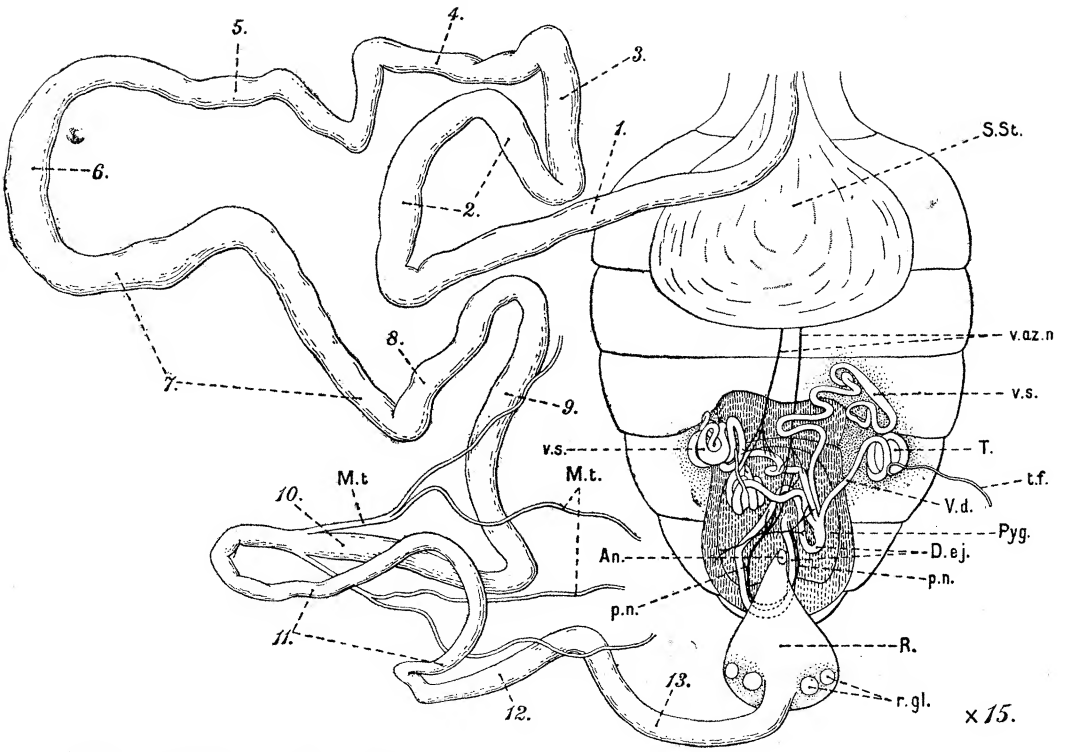

FIG. 5.—Dissection of the Abdomen, showing the Abdominal Intestine unravelled and turned over to the left side, and the Male Genitalia *in situ* in the Abdomen.

S. St., sucking stomach; 1—13, the limbs of the intestine, as indicated in the two previous figures; *M. t.*, *M. t.*, Malpighian tubules; *R.*, rectum; *r. gl.*, rectal glands; *An.*, anus; *T.*, testis; *t. f.*, testicular filament; *V. d.*, vas deferens; *v. s.*, *v. s.*, vesiculæ seminales, that on the left in its natural coil, that on the right unravelled; *D. ej.*, ductus ejaculatorius; *Pyg.*, hypopygium; *v. az. n.*, branches of the ventral azygos nerve (genital nerve); *p. n.*, nerve to penis, following the ductus ejaculatorius.

The ductus ejaculatorius (*D. ej.*) has at its commencement a slight dilatation, into which open the four tubes just described. From this point the ductus runs a very short way backwards, then curves sharply forwards, but soon turns back again, passes across to the left side side of the body, and forms a loop round the rectum, coming forward on the right to pass into the penis.

The various parts of the male generative organs are innervated, as already described, by a nerve plexus formed from the azygos abdominal nerve. There appears to be a small ganglionic swelling on the ductus ejaculatorius, whence arises a nerve (*p. n.*) which follows the ductus in its course to the penis.

The external organs of generation are concealed beneath the hypopygium. The penis is an organ of complicated structure and mechanism, with an

armature of hooks, spines, hairs, and semaphore-like erectile flaps, which would require so many figures to make their arrangement and relations clear, that I refrain at present from attempting any description of them.

The female genital organs differ considerably in appearance according as they are in the gravid or non-gravid condition. In the course of my dissections I have only found one female in the latter state. In the later periods of gestation the condition of the female is obvious externally, but females which do not appear to be gravid are found on dissection to have a small larva in the uterus.

The female organs (fig. 6) consist, like the male, of paired and unpaired portions. The former comprise the ovaries, the receptacula seminis and their ducts, and the uterine glands; the latter are the oviduct, uterus, and

Fig. 6.

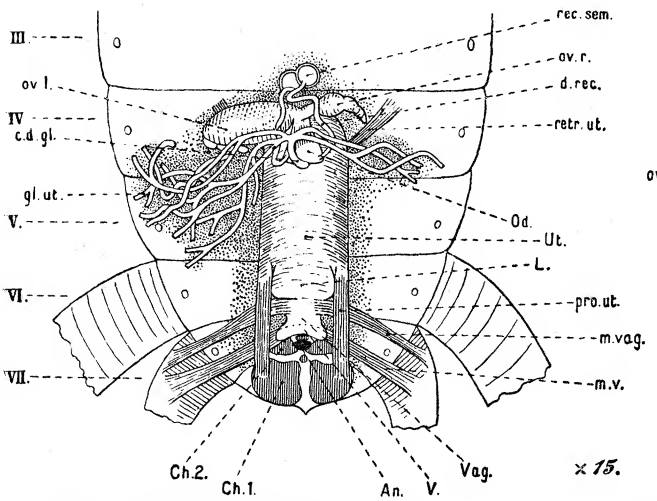

Fig. 7.

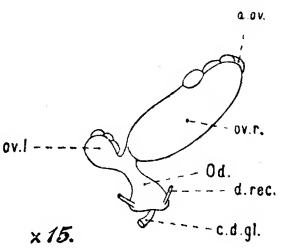

Fig. 6.—The Hinder Segments of the Abdomen with the Female Genital Organs *in situ*, dorsal view.

rec. sem., receptacula seminis; *ov., r., ov. l.*, right and left ovarioles; *d. rec.*, duct of the right receptaculum seminis; *gl. ut.*, uterine glands (the greater number of these have been removed); *c. d. gl.*, their common duct; *retr. ut.*, retractor muscle of the uterus; *Od.*, oviduct; *Ut.*, uterus; *L.*, hinder extremity of the larva, causing a bulge in the uterus; *pro. ut.*, protractor uteri, attached to the chitinous plate (*Ch.* 1); *m. vag.*, muscle (dilator vaginæ?) passing from the vagina to the tergum of the seventh abdominal segment; *m. v.*, muscle passing from the paired chitinous plate (*Ch.* 2) on each side of the vulva to the seventh tergum; *Vag.*, vagina; *V.*, vulva, the anterior margin of which is shown by a dotted line; *An.*, anus; *Ch.* 1, *Ch.* 2, paired chitinous plates.

Fig. 7.—The Ovarioles and Oviduct of a Non-gravid Female.

a. ov., apex of right ovariole; other letters as in the preceding figure. The very large ovum in the right ovariole has pushed the oviduct over towards the left side of the body.

vagina. The female system of organs is considerably modified from the condition usually found in insects, in relation to the fly's peculiar method of reproduction.

The ovaries are reduced to a single pair of ovarian tubes or ovarioles, one on each side of the body (figs. 6 and 7, *ov. r.*, *ov. l.*). Each ovariole shows only a small number of egg-chambers, not more than four or five. The lowest chamber is very much larger than any of the others, and contains a large ovum. When this ovum is comparatively small, the other egg-chambers are in a line with it (fig. 6, *ov. r.*), but as the ovum grows larger it grows past the other egg-chambers, so that they appear attached to the side of the ovum (fig. 6, *ov. l.*, fig. 7., *ov. l.*, *ov. r.*).

The two ovarioles are always asymmetrical, owing to the fact that the ova in the lowest egg-chambers reach full growth on each side alternately, so that if there is a large ovum on the left, there will be a smaller one on the right, and *vice versâ*. The largest ovum I have seen was from a non-gravid female (fig. 7, *ov. r.*), and was probably nearly, if not quite full-sized.

The two ovarioles open into the short, broad oviduct (figs. 6 and 7, *od.*), which widens out at its lower end to open into the uterus slightly behind the proximal end of the latter.

At its distal-expanded end the oviduct receives right and left the two ducts (*d. rec.*) of the receptacula seminis. The latter (*rec. sem.*) are small spherical bodies of a bright orange-yellow colour, surrounded by a whitish, transparent envelope. Examination of the receptacula stained and mounted in Canada balsam shows that the clear envelope is an epithelium of large cells, surrounding a thick chitinous membrane which gives these organs their peculiar colour, and which is too opaque for the contents to be seen except in sections, by which method the receptacula are seen to be filled with spermatozoa. The two receptacula are firmly attached to one another. From each comes off the slender white duct, slightly convoluted. The ducts are perfectly distinct from one another, and open, as described above, into the lower end of the oviduct.

Immediately below the opening of the oviduct into the uterus, a small tube debouches into the latter by a median dorsal aperture. This is the common duct of the uterine glands (figs. 6 and 7, *c. d. gl.*). After a short course it branches right and left into tubes, which branch again repeatedly, forming a great number of glandular tubes, which differ markedly in the gravid and the non-gravid condition. In the latter state the gland-tubes are relatively few and very slender. In the gravid condition, on the other hand, the tubes are very numerous, forming a tightly packed mass filling up the posterior end of the abdomen, and requiring to be pulled away to

show the other parts of the generative system; further, the individual tubes are much thicker, and when stained and mounted, they take up the stain very deeply and appear very opaque. There can be no doubt that these glands serve for the nourishment of the larva in the uterus.

The uterus (*Ut.*) is a large thimble-shaped organ attached to the body-wall by a number of muscles. Two retractors (*retr. ut.*) run forwards from the proximal end. There are two pairs of protractors, one dorsal, the other ventral; the former (*pro. ut.*) start from the sides of the uterus and pass backwards to a pair of chitinous plates (*Ch.* 1) at the posterior end of the body. The wall of the uterus is beset by a very large number of small tracheal tubes (not shown in the figure), and is thick in the non-gravid condition, but becomes thinner when stretched by the growth of the contained larva. In all gravid uteri that I have seen, the two papillæ at the hinder end of the larva cause a bulge in the lower end of the uterus (fig. 6, *L.*). When the larva reaches a certain size, the rings of its segments become plainly visible through the wall of the uterus; they could not be seen in the uterus drawn in fig. 6, but in another, slightly larger, they could be seen distinctly.

The vagina (fig. 6, *Vag.*) is a broad tube, considerably longer in the non-gravid than in the gravid condition, with a pair of dilator muscles (*m. vag.*), which are attached right and left just below its junction with the uterus, and pass outwards to be attached to the anterior margin of the tergum of the seventh abdominal segment. The vagina widens out slightly as it approaches the vulva (*V.*), which is a crescentic, transversely elongated aperture, separated from the anus by a small chitinous plate (*Ch.* 2), one of a pair from which two muscles (*m. v.*) arise and pass outwards to be attached to the seventh tergum, a little way behind the attachment of the vaginal muscles already mentioned. These muscles probably act as dilators of the vaginal aperture, and the five pairs of muscles described in the preceding lines are to be regarded as constituting the mechanism of parturition.

4. *The Vascular System* consists of the heart, in the abdomen, and its continuation, the thoracic aorta, in the thorax.

The heart occupies the five anterior segments of the abdomen, and is situated dorsally immediately below the plates of the terga. It is so imbedded in the fat-body and pericardial tissue that not much can be made out of its structure by dissection alone, and examination of it mounted as a preparation for the microscope is necessary. It can then be seen to have five chambers, each with a pair of ostia and a pair of alary muscles, corresponding to the segments in which it lies. The alary muscles pass out at right angles to the axis of the heart, and can be traced through the fat-body to their attachments at the external lateral margins of the tergal plates.

The hindermost chamber of the heart appears to end blindly posteriorly. A little way in front of the hinder end are attached the two large alary muscles, the largest of the whole series; not far in front of these again are the two ostia, on the sides of the widest part of the chamber. In front of the ostia the lumen of the heart narrows rapidly, and to the narrowed portion is attached the next pair of alary muscles, lying in the hinder part of segment IV. This arrangement is continued in segments II, III, and IV, the dilated portion of the chamber, with the ostia, occupying the middle of the segment, while the alary muscles, attached to the constrictions between the chambers, lie in the posterior regions of the segments. The alary muscles of these three segments are of moderate size. In segment II the heart receives a pair of tracheal tubes, right and left, which come to it opposite the ostia, and fork at once into branches running forwards and backwards. The alary muscles corresponding to the first abdominal segment are very small and difficult to make out, and the region of the heart to which they are attached does not show the slightest diminution or constriction of its lumen, as is the case in all the chambers posterior to it. In front of the first pair of alary muscles, at the usual interval, are the two ostia, quite similar to those of the other chambers. In front of the first pair of ostia the lumen of the heart narrows to form a thin-walled vessel, which passes through the waist to become the artery which I have termed above the thoracic aorta. This last runs along the thoracic intestine on its dorsal side, and is continued over the stomach, remaining apparently quite independent of the digestive tract, and only loosely attached to it, until it reaches the œsophagus. Here it is firmly attached and becomes considerably dilated. A short distance in front of the stomach a conspicuous cushion-like mass of large cells lies over the aorta. At first I took this structure for a ganglion, but it appears to be a sort of lymphatic gland, judging from its appearance in sections. The thoracic aorta is apparently continued through the neck into the head, but I have not been able to follow its course further than the thorax.

The microscopic examination of the heart shows further that its floor is composed chiefly of fusiform cells resembling unstriped muscle-fibres, while its sides are made up of gigantic cells with nuclei of corresponding proportions. These cells are arranged with perfect regularity, and in a manner exactly similar on the two sides of the heart. Each ostium is formed by two cells, which are of small size when compared with the huge cells building up the wall of the heart, but are very large when compared with the cells of the surrounding tissues. Two of the giant cells intervene on each side between the hinder end of the heart and the fifth pair of alary muscles; two more between these muscles and

the ostia next in front of them; and so on with unfailing regularity all the length of the heart, each ostium being separated from the alary muscles next in front or behind by just two giant cells. In front of the first pair of ostia are found two cells of the usual size on each side, then a pair of slightly smaller cells, which pass on into the walls of the thoracic aorta. Thus the entire wall of the heart is built up of 23 pairs of giant cells, not counting the ten couples of smaller cells which compose the five pairs of ostia; to wit, four pairs to each of the five chambers, two additional pairs behind the fifth pair of alary muscles, and one pair anteriorly, making the transition to the thoracic aorta. In view of the fact that the thoracic vessel is itself to be considered as a modified anterior portion of the heart, it is interesting to find that its delicate wall contains very large, flattened nuclei, arranged in pairs, right and left.

The alary muscles consist of delicate fibrils, arranged in an irregular fan-like manner, uniting into a stout muscle-fibre which is distinctly striated.

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